

**First record of the genus *Anadia* (Reptilia: Squamata: Gymnophthalmidae)
from Guyana based on an enigmatic specimen from
Mount Kopinang, Wokomung Massif**
Primeiro registro do gênero *Anadia* (Reptilia: Squamata: Gymnophthalmidae)
para Guyana baseado em um enigmático exemplar do monte
Kopinang, maciço de Wokomung

Philippe Jacques Robert Kok^{I, II}, Donald Bruce Means^{III}, Gilson Antonio Rivas^{IV}

^IRoyal Belgian Institute of Natural Sciences. Bruxelas, Bélgica

^{II}Vrije Universiteit Brussel. Bruxelas, Bélgica

^{III}Coastal Plains Institute and Land Conservancy. Tallahassee, Flórida, USA

^{IV}Universidad del Zulia. Museo de Biología. Maracaibo, Venezuela

Abstract: We provide the first record of the lizard genus *Anadia* (Gymnophthalmidae) from Guyana, based on an enigmatic specimen collected in the Pakaraima Mountain Range and provisionally referred to *Anadia escalerae*, a species described from a single specimen collected in the highlands of the Venezuelan Guayana. The new locality extends the known distribution of the genus *Anadia* to approximately 300 km to the SE and represents the easternmost known record for an *Anadia* species. The collected specimen is described in detail, compared to other known *Anadia* species, and closely compared to the holotype of *Anadia escalerae*, from which it differs in several characteristics that are discussed.

Keywords: *Anadia escalerae*. Distribution extension. Pantepui. Guyana. Wokomung Massif. Venezuela.

Resumo: Registra-se, pela primeira vez, um lagarto do gênero *Anadia* para a Guiana, com base em um exemplar enigmático coletado nas montanhas Pakaraima. Este exemplar é provisoriamente atribuído a *Anadia escalerae*, uma espécie descrita através de um único indivíduo coletado nas montanhas da Guayana venezuelana. Esta nova localidade de ocorrência amplia a distribuição do gênero *Anadia* por cerca de 300 km na direção sudeste, representando o registro mais oriental para o gênero. O exemplar é descrito em detalhe, comparado com demais espécies de *Anadia* e, especialmente, com o holotipo de *A. escalerae*, do qual difere em vários aspectos que são discutidos.

Palavras-chave: *Anadia escalerae*. Ampliação da distribuição. Pantepui. Guyana. Maciço de Wokomung. Venezuela.

KOK, P. J. R., D. B. MEANS & G. A. RIVAS, 2013. First record of the genus *Anadia* (Reptilia: Squamata: Gymnophthalmidae) from Guyana based on an enigmatic specimen from Mount Kopinang, Wokomung Massif. **Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais** 8(1): 27-39.

Autor para correspondência: Philippe Jacques Robert Kok. Royal Belgian Institute of Natural Sciences. Department of Vertebrates. Rue Vautier 29, B-1000. Bruxelas, Bélgica (philippe.kok@naturalsciences.be).

Recebido em 20/03/2013

Aprovado em 29/04/2013

Responsabilidade editorial: Marinus Hoogmoed



INTRODUCTION

Pantepui is a remarkable biogeographical region lying in the northwestern part of the Guiana Shield, renowned for its impressive vertical-sided table mountains (tepui) made of Precambrian sandstone that rise above the savannah and tropical forest. Although the region is traditionally seen as one of the foremost areas of endemism in the Neotropics (Berry *et al.*, 1995; Davis *et al.*, 1997), it has been recently demonstrated that despite their current unique geomorphology the tepui were insufficient barriers to local (*i.e.* within Pantepui) gene flow leading to a low genetic diversity among tepui summit amphibians and reptiles (Kok *et al.*, 2012). Many parts of the region are unexplored scientifically, but even the most visited areas still bring interesting findings, helping to better understand the origin and evolution of the Pantepui biota.

The primarily North Andean genus *Anadia* Gray, 1845 currently consists of 18 species (Myers *et al.*, 2009; Kok & Rivas, 2011; Rivas *et al.*, 2012b) mostly distributed in Costa Rica and Panama, and along a southwest-northeast arc which connects the Northern Andes in Ecuador to the Colombian Andes and the Eastern Coastal Range in Venezuela. More than half of the currently known species are from Venezuela (Rivas *et al.*, 2012a), suggesting a possible centre of radiation for the genus in that region. Only two species are reported from south of the Río Orinoco in the highlands of the Venezuelan Guayana, namely *Anadia escalerae* Myers, Rivas Fuenmayor & Jadin, 2009, known from a single female specimen from La Escalera (*ca.* 1430 m elevation), Bolívar state, Venezuela, and *Anadia mcdiarmidi* Kok & Rivas, 2011, known from three tepui summits in the Chimantá massif (*ca.* 2,100-2,600 m elevation), Bolívar state, Venezuela (Rivas *et al.*, 2012a). The only comprehensive review of the genus is that of Oftedal (1974), which includes only 11 of the currently known species, arranged in five species groups primarily distinguished by the condition of scalation and femoral pores. Recent new species descriptions (Myers *et al.*, 2009; Kok & Rivas, 2011), revalidation of *Anadia pamplonensis*

(Harris & Ayala, 1987), new distributional records (García-Pérez & La Marca, 1989), as well as new data about poorly known species (Rivas *et al.*, 2012b) contributed to a better systematic knowledge of the genus.

More than seven years ago, in June 2005, Les Minter (Western Cape, South Africa) showed PJRK a photograph of an uncollected putative *Anadia* species observed in August 2004 in the northern Pakaraima Mountain Range of Guyana. That photograph was puzzling because no species of *Anadia* had ever been reported from Guyana, and at that time no species had been described from south of the Río Orinoco. Since then, several expeditions have been conducted in the Pakaraima Mountain Range of Guyana by two of us (PJRK and DBM) and by colleagues, but all were unable to collect any *Anadia* specimen. However, in June 2012, DBM accidentally secured a specimen from Mount Kopinang in the Wokomung massif, a sandstone massif in the Pakaraima mountains of Guyana. Unfortunately the single specimen available was unwittingly squashed by a porter and is in poor condition, but its generic assignation is not in doubt. Given that the genus *Anadia* has never been reported from Guyana (Cole *et al.*, 2013), the extreme rarity of these lizards in the region, and the small chance that additional specimens could be collected in the near future, we provide a complete description of this specimen, which we provisionally (and conservatively) refer to *Anadia escalerae* (see comments under Species allocation).

MATERIALS AND METHODS

Soon after having been accidentally stepped upon, the specimen was fixed in 95% ethanol. It was later transferred to 70% ethanol for permanent storage, with a piece of muscle tissue removed and preserved in 95% ethanol for molecular study. The specimen has been deposited in the collections of the Institut Royal des Sciences Naturelles de Belgique (IRSNB), Brussels, Belgium.

Coordinates and elevations of the collection locality were acquired using a Garmin Global Positioning System unit and referenced to map datum WGS84.



Comparisons of external character states are based both on original descriptions, pertinent literature, and examination of museum specimens (see Appendix for additional material examined). Terminology for morphological characters and scale counts follow Oftedal (1974), Kizirian (1996), Myers *et al.* (2009), and Kok & Rivas (2011). All morphometric data were taken from the preserved specimen to the nearest 0.01 mm and rounded to the nearest 0.1 mm, under a Leica stereo dissecting microscope using an electronic digital calliper. For ease of comparison, the specimen description mainly follows the pattern of Myers *et al.* (2009) and Kok & Rivas (2011). The following measurements and scale counts were taken and abbreviated as follows: (1) snout-vent length, from tip of snout to posterior margin of vent (SVL); (2) tail length, from posterior margin of vent to tip of tail (TL); (3) head length, from tip of snout to anterior margin of ear opening (HL); (4) greatest width of head (HW); (5) greatest depth of head (HD); (6) snout-axilla length (SAL); (7) neck length, from posterior edge of ear opening to forearm held at right angle to body (NL); (8) axilla-groin distance (= trunk length), from base of forelimb to base of hind limb (AXG); (9) forelimb length, from axilla to tip of claw of longest digit (FIL); (10) hind limb length, from groin to tip of claw of longest digit (HIL); (11) number of middorsal scales, from postoccipitals to the level of posterior edge of thigh held at right angle to body (MD); (12) number of ventrals in longitudinal rows, counted at midbody and including small ventrolateral rectangular plates (VL); (13) number of ventrals in transverse rows, counted between collar and vent [thus including preanals, which as pointed out by Oftedal (1974) are frequently difficult to distinguish from ventrals in the genus] (VT); (14) number of scales around midbody, counted at mid-distance between collar and vent (SAM); (15) number of supralabials (SL); (16) number of infralabials (IL); and (17) number of femoral pores under each thigh (FP).

Sex was determined by the absence of hemipenes (base of tail dissected) and direct examination of gonads.

Taxonomy follows Oftedal (1974), Pellegrino *et al.* (2001), and Rodrigues *et al.* (2005). Institutional acronyms mostly follow Frost (2013) and are as follows: EBRG = Museo de la Estación Biológica Rancho Grande, Maracay, Aragua, Venezuela; IRSNB = Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MBLUZ = Museo de Biología de la Universidad del Zulia, Zulia, Venezuela; MHNLS = Museo de Historia Natural La Salle, Caracas, Venezuela; ZMB = Museum für Naturkunde, Humboldt Universität, Berlin, Germany.

RESULTS

SPECIMEN DESCRIPTION

Anadia cf. escalerae Myers, Rivas Fuenmayor & Jadin 2009

Voucher specimen. IRSNB 18305 (field number CPI-10711), an adult female with small ovarian eggs collected by D. Bruce Means and Talesha Nurse, 17 June 2012, SE side of Mount Kopinang, Wokomung Massif, Potaro-Siparuni District, Guyana (04° 04' 50" N, 59° 52' 43" W, 1,385 m elevation).

Generic allocation. The specimen is placed in the genus *Anadia* because it fits most of the 11 diagnostic traits for the genus proposed by Oftedal (1974) (differences are between brackets): dorsal scales smooth, essentially homogeneous; no distinct rows of much smaller scales between lateral scales; ventral scales smooth, quadrangular; head scales smooth, without striation; single frontonasal separating nasals; paired prefrontals; a large unpigmented and undivided palpebral disc [divided in several large scales according to Oftedal (1974)]; gular scales smooth, essentially homogeneous, with no distinctly enlarged longitudinal rows; seven large preanal scales; adult female with small femoral pores; limbs well developed, pentadactyl with all toes clawed.

Species allocation. The specimen may be immediately distinguished from *Anadia ocellata*, *A. vittata*, *A. rhombifera*, and *A. petersi* [all members of the

ocellata group of Oftedal (1974)] and *A. bogotensis* [the only member of the *bogotensis* group of Oftedal (1974)] in having quadrangular dorsal scales (subhexagonal in species of the *ocellata* group, imbricate in *A. bogotensis*), and in lacking a subnostril groove or divided nasal (nasal divided or subnostril groove present in species of the *ocellata* group and in *A. bogotensis*); from *A. altaserrania* [a member of the *bitaeniata* group of Oftedal (1974) according to Harris & Ayala (1987)] in having prefrontals (lacking in *A. altaserrania*), and in having a higher number of middorsal scales (61 vs. 45-47 in *A. altaserrania*); from *A. bitaeniata*, *A. brevifrontalis*, *A. hobarti*, *A. pamplonensis*, and *A. pulchella* [all members of the *bitaeniata* group of Oftedal (1974) according to La Marca & García-Pérez (1990)] in having a higher number of middorsal scales (61 vs. a maximum of 50 in species of the *bitaeniata* group); from *A. blakei* and *A. marmorata* [members of the *marmorata* group of Oftedal (1974)] in having a much higher number of middorsal scales (61 vs. less than 35 in *A. blakei* and *A. marmorata*); from *A. bumanguesa* [a member of the *bitaeniata* group of Oftedal (1974) according to Rueda-Almonacid & Caicedo (2004), but a possible synonym of *A. steyeri* and thus a member of the *steyeri* group of Oftedal (1974) according to Rivas *et al.* (2012b)] in having a lower number of scales around midbody (36 vs. 40-41 in *A. bumanguesa*); from *A. steyeri* [the only member of the *steyeri* group of Oftedal (1974), but see Rivas *et al.* (2012b)] in having a lower number of scales around midbody (36 vs. 41-45 in *A. steyeri*), and in having a higher number of ventrals in transverse rows (41 vs. 34-37 in *A. steyeri*); from *A. pariaensis* (not assigned to any species group in the original description) in having a lower number of middorsal scales (61 vs. 70-72 in *A. pariaensis*), in having a higher number of ventrals in transverse rows (41 vs. 36-37 in *A. pariaensis*), and in having a lower number of scales around midbody (36 vs. 41-42 in *A. pariaensis*); from *A. steyeri* [the only member of the *steyeri* group of Oftedal (1974), but see Rivas *et al.* (2012b)] in having a higher number of ventrals

in transverse rows (41 vs. 34-37 in *A. steyeri*), and in having a lower number of scales around midbody (36 vs. 41-45 in *A. steyeri*); from *A. mcdiarmidi* (not assigned to any species group in the original description), one of the two geographically closest relatives (with *A. escalerae*), in having a slender body (robust in *A. mcdiarmidi*), a higher number of middorsal scales (61 vs. 53-57 in *A. mcdiarmidi*), in having a much higher number of ventrals in transverse rows (41 vs. 29-31 in *A. mcdiarmidi*), in having four large postparietals (vs. 6-8 variable in size in *A. mcdiarmidi*), and in having large flat scales on the side of the neck (vs. small pebble-like scales in *A. mcdiarmidi*).

The specimen best fits description by Myers *et al.* (2009) of *Anadia escalerae* in having similar proportions and scale counts (see Table 1), but it differs from the holotype and single known specimen of *A. escalerae* by a combination of characters that could be diagnostic for this species (see below). However, we refrain from describing it as a new taxon, given that the only specimen collected is in poor state of preservation, and that *A. escalerae* was also described based on a single specimen reported as being damaged [found dead, partly eaten by insects, see Myers *et al.* (2009)]. Our knowledge of intraspecific variation in *A. escalerae* is thus non-existent. Our conservative action is also justified by the fact that *A. escalerae* has been described from a locality situated about 300 km airline from the new locality, within the same biogeographic area.

The specimen from Mount Kopinang (Figures 1-3) mainly differs from the holotype of *Anadia escalerae* (characters of the latter between parentheses, confirmed by a thorough re-examination of the holotype by GR) in having:

- (1) Undivided lower eyelid in adult (divided in four vertical panes);
- (2) Smooth dorsal scales (several being weakly, but distinctly, keeled);
- (3) Thirty-six scales around midbody (40);
- (4) Four large postparietals (eight medium-sized). Several gymnophthalmid genera are well known for their high intraspecific variability in head scalation (*e.g.*



Table 1. Sex, measurements (in mm) and scale counts of *Anadia escalerae*.

	Holotype (EBRG 1998) La Escalera, Venezuela	IRSNB 18305 Mount Kopinang, Guyana	Uncollected Waranau Mountain, Guyana
Sex	Adult female	Adult female	-
SVL	63.0	66.7	-
TL	102.0+ (-tip)	123.0	-
HL	12.7	13.7	-
HW	7.2	7.1	-
HD	4.5	4.7	-
SAL	23.0	24.3	-
NL	8.5	8.5	-
AXG	34.0	35.9	-
FIL	14.0	13.2	-
HIL	21.0	21.6	-
MD	63	61	61
VL	12	15	-
VT	34 [39 ¹]	41	-
SAM	40	36	-
SL	7	7	-
IL	5	5	-
FP	10/5 ²	9/10 ²	-

¹ Number in bracket obtained by our method for counting ventral scales, which slightly differs from that used by Myers *et al.* (2009).

² Numbers correspond to right/left side; abbreviations are defined in the text.

Donnelly *et al.*, 1992; Kok & Rivas, 2011), and the number of postparietals seems not always intraspecifically consistent in *Anadia* (the authors, personal observation), this character could be variable in *A. escalerae*;

(5) Two pairs of genials (three pairs, see Figure 4). Due to poor preservation and problems of clearly distinguishing sutures from scars, we cannot exclude that the first left genial is fused with the mental in the specimen from Mount Kopinang. A similar fusion is observed in a specimen of *Anadia bogotensis* (ZMB 69116);

(6) Enlarged postgenial in point-contact with the last infralabial (broad contact, see Figure 4). The nature of the

median contact between some head scales apparently varies intraspecifically in the genus. In *Anadia bogotensis* for instance the postgenial may or not be in contact with infralabials (PJRK, personal observation);

(7) Nasal in contact with the rostral (separated by first supralabial, see Figure 4). The nature of the nasal-rostral contact varies intraspecifically in *Anadia*. This is especially evident when several specimens of a same species are available for comparisons. PJRK examined 13 specimens of *A. bogotensis* (see Appendix), and five of these specimens (38%) have the nasal separated from the rostral by the first supralabial (in contact in other specimens).

Voucher description. An adult female in poor condition, having been accidentally squashed and subsequently fixed in 95% ethanol, which led to desiccation of soft body parts (Figures 1-3), with 66.7 mm SVL and 123.0 mm TL. A slender *Anadia* species with moderately short limbs (digits do not overlap when limbs are adpressed along body). Snout attenuate, flat in profile. HL 21% of SVL; head approximately 1.9 times longer than wide, approximately 1.5 times wider than high; head conspicuously wider than neck. Neck long, 62% of HL, 24% of AXG. SAL 68% of AXG, 36% of SVL. Body wider than deep. Tail dorsoventrally flattened, about 1.8 times longer than SVL. Limbs pentadactyl with all digits clawed. Forelimb 20% of SVL, 37% of AXG; hind limb 32% of SVL, 60% of AXG.

Scutellation on the dorsal surface of head (Figure 2) is typical for the genus (see figure 1 in Oftedal, 1974). Head scales are smooth with a few (1-9) minute scattered dark pits located on the posterior and lateral margins of postparietals (= occipitals), postoccipitals, and most temporals. Pits are also found on the posterior margin of most dorsal scales.

Rostral much wider than deep, laterally in contact with nasals and first supralabial, dorsally in contact with large frontonasal. Frontonasal with nearly straight, slightly concave anterior margin, posteriorly pointed. Paired prefrontals in contact, medial suture relatively short.





Figure 1. Dorsal (left) and ventral (right) views of the preserved adult female *Anadia* cf. *escalerae* (IRSNB 18305) from Mount Kopinang, Guyana. Photos: Philippe J. R. Kok.

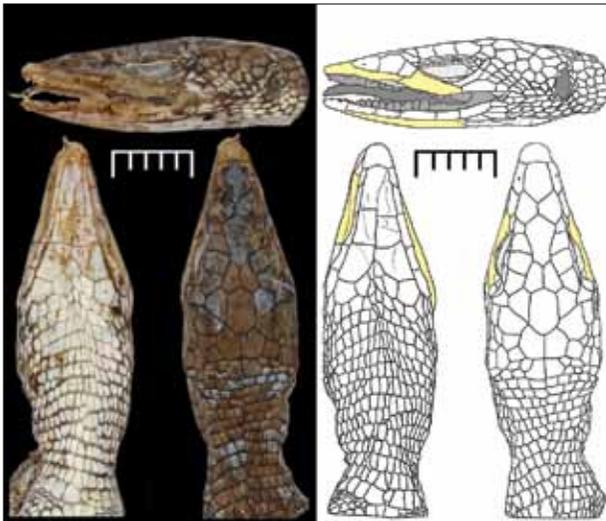


Figure 2. Lateral, ventral, and dorsal views of the head of the preserved *Anadia* cf. *escalerae* (IRSNB 18305) from Mount Kopinang, Guyana. Parts in yellow are too damaged to be drawn. Scale lines = 5 mm. Photos: Philippe J. R. Kok.

Frontal much wider anteriorly, with blunt anterior point, posteriorly pointed. Paired frontoparietals with long medial suture (2.6 times the length of prefrontal medial suture), in contact with interparietal, parietals, and two posterior supraoculars. Three large supraoculars subequal in size, one small presupraocular situated between prefrontal and first supraocular. Interparietal longer than wide, rounded posteriorly. Parietals longer than wide, as wide as interparietal, not extending as far as interparietal posteriorly. A series of four large postparietals (occipitals), subequal in size, circling the common posterior margin of parietals and interparietal.

Nasal scale entire, in contact with rostral, posteriorly in contact with prefrontal, and in broad contact with loreal. Loreal large, pentagonal, in contact with first superciliary and frenocular, in point contact with presupraocular on right side

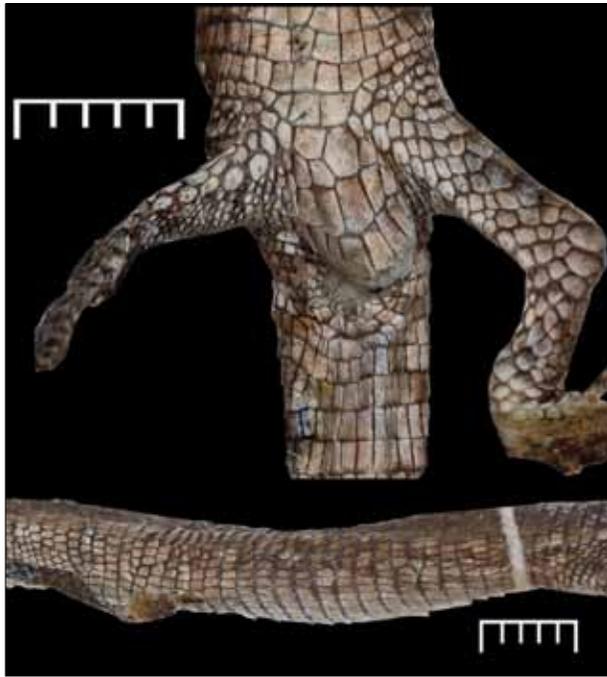


Figure 3. Subpelvic region (above) of the preserved adult female *Anadia cf. escalerae* (IRSNB 18305) from Mount Kopinang, Guyana, showing preanal scales, femoral pores, and trunk (below) of the same specimen in lateral view (head to the left), showing scalation at midbody. Scale = 5 mm. Photos: Philippe J. R. Kok.

only (note: contacts between scales are sometimes difficult to evaluate because of the preservation state of the specimen). One small preocular, three postoculars. First superciliary small, followed by three larger superciliaries. No small azygous scale between superciliaries and supraoculars. Frenocular followed posteriorly by four suboculars on right side (condition undetermined on the left side due to preservation state). Third subocular slightly extending towards lip between supralabials four and five on the left side (condition undetermined on the right side due to preservation state). Suboculars separated from palpebral by a few scattered, mostly inconspicuous, tiny scales. Seven supralabials on right side, condition undetermined on left side.

Eight ciliaries along upper eyelid. Moveable lower eyelid with translucent undivided palpebral disc on both sides.

Temporal scales subimbricate, smooth, with flat surfaces, slightly larger above and smaller below. Ear

opening broad, ovoid, slightly inclined posterodorsally, edged with small, slightly pebble-like scales; tympanum recessed, pigmented.

Underside of head (Figure 2) with five infralabials on each side. A large mental followed by a large postmental in contact with first two infralabials. Two pairs of large genials (we cannot exclude that a genial is fused with the postmental), first pair in broad contact medially, second pair in short contact anteromedially, separated by two scales posteromedially, pairs of genials in lateral contact with infralabials 3-5; one pair of postgenials, in contact with last genial and in broad contact with infralabial 5, medially separated by four scales. Gulars subequal in size, arranged in transverse rows. Well-defined collar row of ten mostly subequal scales, except the median one that is much smaller; no distinctly enlarged longitudinal rows. Side of neck between ear and collar having subequal subimbricate scales with flat surfaces.

Middorsal scales 61. Dorsal scales on neck juxtaposed, irregularly shaped, with flat surfaces. Dorsal body scales smooth, juxtaposed, mainly quadrangular, a few irregularly shaped, but most are longer than wide, in transverse rows only. Lateral scales smooth, similar to dorsals and subequal in size (Figure 3).

Ventral scales wider than dorsals, smooth, juxtaposed, quadrangular, longer than wide, except for a few square scales on anterior belly; in 15 longitudinal rows at midbody and 41 transverse rows between collar and vent.

Seven marginal preanal scales anterior to vent, the middle two slightly wider than the adjacent lateral ones. Femoral pores small, in unswollen pore scales mostly in linear contact; ten pores on left thigh, nine on right. Pores do not extend onto preanal area (Figure 3).

Caudal scales smooth, subimbricate, rectangular, in transverse rows around tail. Most dorsal caudal scales with 1-3 dark pits on the posterior margin of scales.

Scales on dorsal surfaces of arm large, smooth, imbricate; ventral surfaces of arm with similar, but smaller and less imbricate scales. Hind limbs with large, smooth

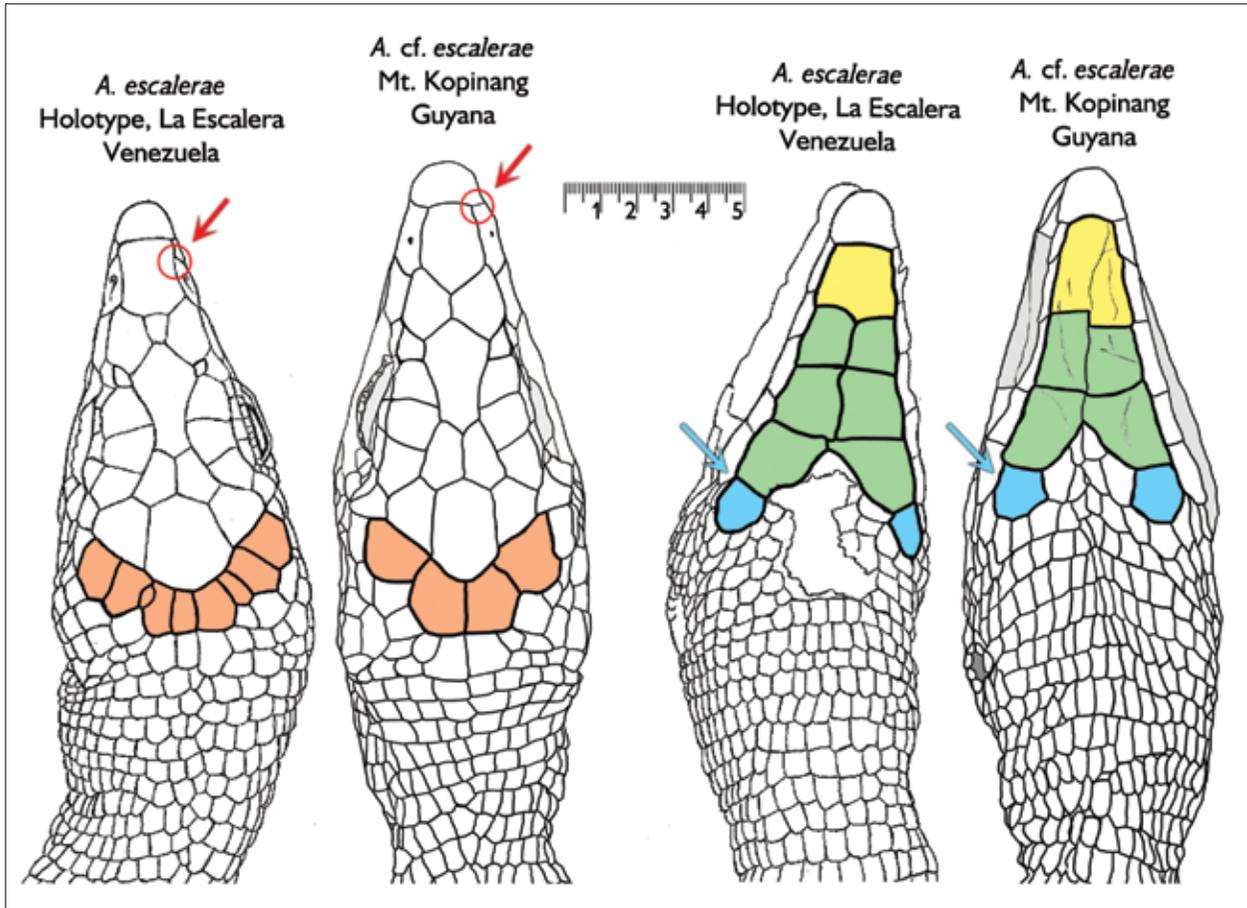


Figure 4. Comparison of head scalation in the female holotype of *Anadia escalerae* from La Escalera, Venezuela (EBRG 1998), and the female specimen from Mount Kopinang, Guyana (IRSNB 18305). Red arrow and red circle highlight the absence of contact between the nasal and rostral in the holotype vs. contact in the specimen from Mount Kopinang. Postparietals are in light orange, postmental in light yellow, genials in light green, and postgenials in light blue, the blue arrow showing contact zone with last infralabial. Drawing of the head of the holotype of *A. escalerae* modified from Myers *et al.* (2009). Scale in mm.

subimbricate to imbricate scales on anterior face of thighs and on lower legs; scales similar but smaller on ventral side of thigh. Dorsal and posterior aspects of thigh with much smaller, irregularly shaped juxtaposed scales.

Lengths of hands and feet measurable, but extremities are too damaged for detailed description.

Tongue lanceolate; proximal three-fourths unpigmented and attached to the buccal floor, distal one-fourth free, pigmented, including forked part. Upper surface behind the forked part covered with imbricate scale-like papillae that extend onto ventrolateral parts of tongue. No

structure visible on the lower surface of the tongue, except a very shallow medioventral groove.

Anterior maxillary and dentary teeth conical, unicuspid, with feeble recurvature, becoming larger posteriorly. Posteriormost teeth weakly bi- or tricuspid.

Colour in life. Dorsum appeared totally black in hand in the field in subdued light, slightly lighter ventrally.

Colour in preservative. After approximately seven months in preservative, the dorsal surfaces are brown, the ventral surfaces are light grey. Tympanum is dark brown. About a dozen faint ocelli two scale rows wide

visible dorsolaterally on the trunk between the limbs and extending along the sides of the tail to its tip.

Habitat. The lizard was found writhing in a footprint in deep, black, wet, peaty soil next to a small-diameter, fallen rotting log where it may have been hiding. Habitat was closed-canopy cloud forest with abundant epiphytes on tree trunks and branches, especially an olive green pendant moss (Figure 5). Ground cover was deep leaf and branch litter on perennially wet, black peaty soil. The collecting site was a 1,385-m elevation terrace on the southwest flank of Mount Kopinang. It receives abundant rainfall and mists with daily maximum temperatures between 10-15 °C.

DISCUSSION

The specimen from Mount Kopinang extends the known distribution of *Anadia* about 300 km to the SE representing the easternmost record of the genus, and the first formal record of an *Anadia* species in Guyana.

An additional *Anadia* specimen was photographed (Figure 6), but unfortunately not collected, on Waranau Mountain in the Pakaraima Mountain Range of Guyana (06° 08' 11" N, 60° 22' 45" W, 695 m elevation, see Figure 7) in August 2004. Based on the photograph, the specimen presents a similar count of dorsal scale rows (61, counted on a high resolution photograph) and a similar pattern of postparietals (4 large postparietals), and is provisionally referred to *Anadia escalerae* as well.

Many genera of the family Gymnophthalmidae are well known for their high intraspecific variability in head scalation, and the genus *Anadia* confirms the rule. We do not believe that the nature of the median contact between prefrontals and the presence/absence of an azygous scale between these scales should be used as diagnostic characters in *Anadia* (*contra* Myers *et al.*, 2009). Indeed, two of the specimens of *A. marmorata* we examined have the prefrontals in point contact (ZMB 1161 from Puerto Cabello, Venezuela, and EBRG 5798 from Parque Nacional Macarao, Venezuela) while in

others (e.g. MBLUZ 1170 from Parque Nacional Macarao, Venezuela, and MBLUZ 1231 from Rancho Grande, Venezuela) prefrontals are in broad contact. Likewise, an individual of *A. bogotensis* (ZMB 69117) has an azygous scale between the prefrontals, in contrast with other conspecific specimens examined, including from the same locality (Cundinamarca, Colombia, see Appendix).

Taken separately, most of the possible diagnostic characters between *Anadia escalerae* and the specimens from the Pakaraima Mountain Range of Guyana show variability within the genus. Additional material is necessary to assess if these characters are variable in *A. escalerae*, and specifically to assess whether the combination of these characters could be used to identify the specimen from Mount Kopinang as a distinct species.

The monophyly of *Anadia* has not been properly tested yet, and phylogenetic relationships between species remain unknown (Kok & Rivas, 2011). Overall similarities and high dorsal scale counts suggest a possible close relationship between *Anadia escalerae* and *A. pariaensis*, the latter known only from the Eastern Coastal range of Venezuela, ca. 500 km NNW from the type locality of *A. escalerae*.

ACKNOWLEDGEMENTS

We thank I. Ramdass and the Guyana Environmental Protection Agency for Biodiversity Research Permit #061212 BR 020 and Permission to Export Biological Specimens for Taxonomic Analysis #072412 SP 054, P. Sukhai of the Guyana Ministry of Amerindian Affairs for permission to enter the Patamona Amerindian village of Kopinang, and W. Edwin (Tushau), the village council, and the friendly people of Kopinang Village for permission to lodge overnight in their guesthouse and travel through their lands. DBM thanks R. Downes and the men of Kopinang Village for organizing and carrying his equipment and food to the summit of Mount Kopinang, setting up his camp, and working for him. We thank T. Nurse, DBM Guyanese student local counterpart, for her scientific



Figure 5. Habitat of *Anadia* cf. *escalerae* on the SE side of Mount Kopinang, Wokomung Massif. A: Closed-canopy cloud forest where the specimen was collected; note the black, peaty soil. B: Abundant vegetation with epiphytes and mosses on tree trunks and branches at the same locality. Photos: D. Bruce Means.



Figure 6. *Anadia* cf. *escalerae* in life (not collected), photographed on 11 August 2004 on Waranau Mountain in the Pakaraima Mountain Range of Guyana at an altitude of 695 m. Photo: Les Minter.

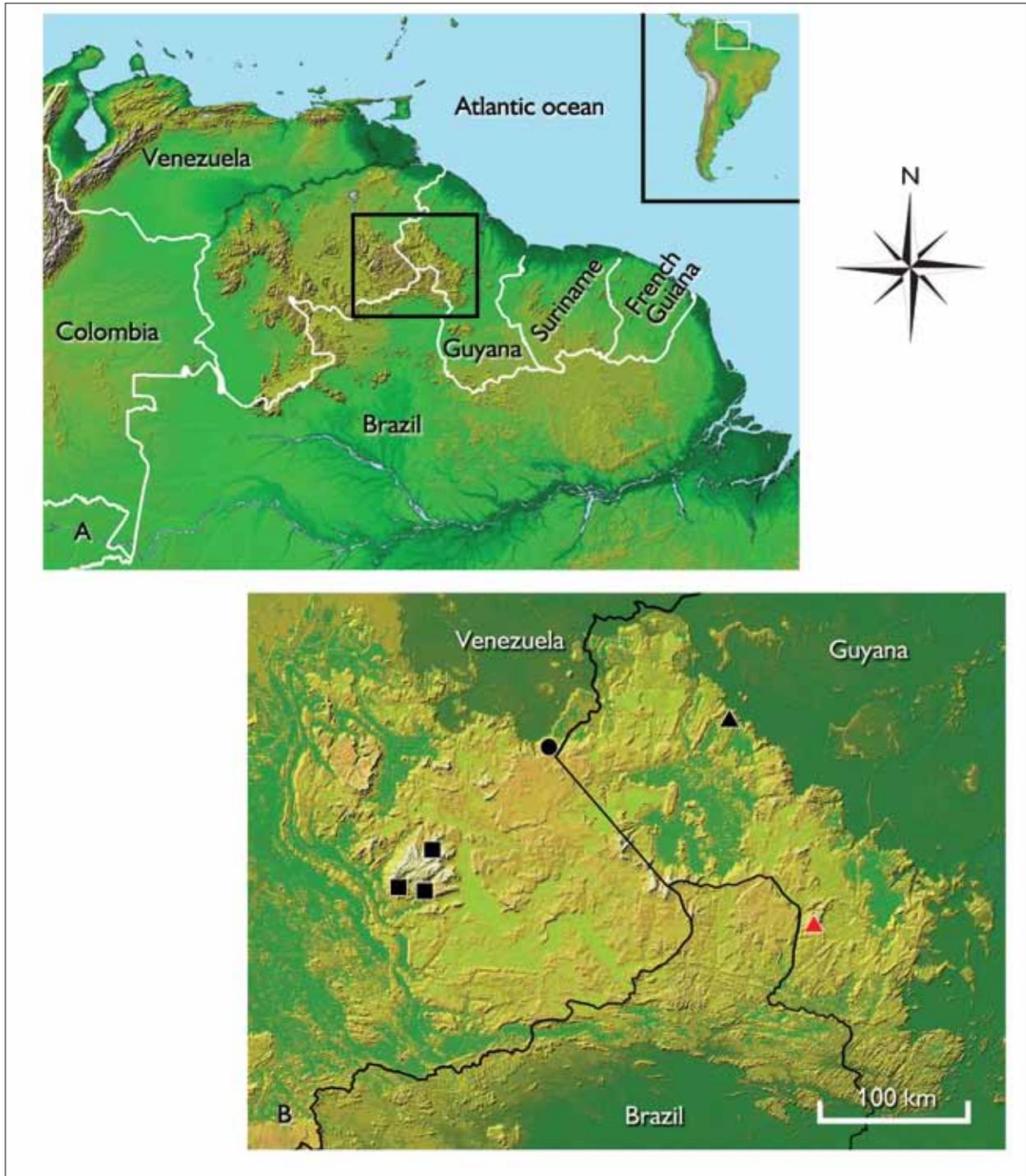


Figure 7. Map of the Guiana Shield region (A), with enlarged black rectangle corresponding to the Eastern Pantepui Region (B). Red triangle corresponds to Mount Kopinang from where the Guyanese voucher specimen of *Anadia* cf. *escalerae* was obtained, black triangle corresponds to the Waranau Mountain where a second specimen has been photographed in 2004, black dot corresponds to La Escalera, type locality of *A. escalerae*; black squares indicate the known distribution of *A. mccliamidi*, the only other *Anadia* species reported from south of the Río Orinoco.



and field assistance, and L. Minter for the photograph of a specimen from Waranau Mountain in Guyana. M. S. Hoogmoed and two anonymous reviewers made useful comments on an earlier version of the manuscript. PJRK warmly acknowledges R. Ernst (SNSD) for hospitality and working space during his visit to the Museum für Tierkunde in Dresden, Germany. We thank M.-O. Rödel and F. Tillack (SMNS), and F. Bisbal and E. Camargo (EBRG) for letting us examine specimens under their care. This research was funded by National Geographic Expeditions Council Grant #EC0504-11.

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APPENDIX. Additional material examined.

Anadia bitaeniata – (1) VENEZUELA: Mérida: Parque Nacional Sierra La Culata, ZMB 18214.

Anadia blakei – (1) VENEZUELA: Sucre: Cerro Humo, Península de Paria, EBRG 2746.

Anadia bogotensis – (16) COLOMBIA: Cundinamarca: Santa Fé de Bogotá, ZMB 4654-60, ZMB 69111-18 (syntypes of *Ecpleopus bogotensis*); Bogotá, ZMB 30043.

Anadia escalerae – (1) VENEZUELA: Bolívar: La Escalera, ca. 1,430 m, 132 km SE Río Cuyuní (= 46 km SE km 88) on the road to Santa Elena de Uairén, EBRG 1998 (holotype).

Anadia marmorata – (5) VENEZUELA: Aragua: Estación Biológica de Rancho Grande, 1,100 m, MBLUZ 1231 (formerly EBRG 3423); La Colonia Tovar, MBLUZ 1233. Carabobo: Puerto Cabello, ZMB 1160 (syntype of *Gerrhonotus*

poecilochilus). Distrito Capital: Sector Jerenba Parque Nacional Macarao, 2,300 m, EBRG 5798. Miranda: Carretera Panamericana, km 11, Instituto Venezolano de Investigaciones Científicas (IVIC), centro de ecología, EBRG 5919.

Anadia mcdiarmidi – (4) VENEZUELA: Bolívar: Abakapá-tepui, 2,201-2,242 m, IRSNB 2677 (holotype), IRSNB 2674-76 (paratopotypes).

Anadia steyeri – (2) VENEZUELA: Carabobo: Puerto Cabello, ZMB 24293 (holotype). Yaracuy: Hacienda El Zinc, Serranía de Aroa, 1,200 m, EBRG 5995.

Euspondylus acutirostris – (3) VENEZUELA: Aragua: Carretera El Junquito-Colonia Tovar, a 1.5 km a la derecha del arco de la Colonia Tovar, 2,350 m, MHNLS 17474. Falcón: Sierra de San Luis, cerro Galicia, La Soledad, 1,200 m. MBLUZ 1232 (formerly EBRG 3971). Yaracuy: Pico el Tigre, Parque Nacional Yurubí, 1,700 m, EBRG 5857.

